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Research Article

Leaf trait network structure drives the invasion success of *Sonneratia apetala* in Guangxi mangroves

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Abstract

Mangrove forests are vital blue carbon ecosystems that offer carbon sequestration, coastal protection, and biodiversity support. In China, native mangrove communities have become increasingly fragmented and are losing functional diversity due to anthropogenic disturbance. Since the 1980s, introduced *Sonneratia apetala* Buch.-Ham. has been widely used in restoration. Although it has established rapidly and aided early revegetation, it has spread along the southern coast and suppressed native species. The trait-based mechanisms underpinning the competitive advantage of *S. apetala* and the consequences for native functional diversity–remain unclear. We compared 17 leaf functional traits from five native mangrove species and introduced *S. apetala*, employing a functional trait network (FTN) approach to analyze the structural and variability patterns of leaf trait networks. The FTN framework visualized the relationships among traits as nodes and edges, enabling a comprehensive understanding of how multi-trait coordination drives ecological strategies. The connectivity and centralization of the *S. apetala* leaf trait network were higher than those of native species, forming a "centralized-efficient" strategy, in contrast to a "dispersed-cooperative" strategy of native species. The efficient resource-use system of *S. apetala* was based on high chlorophyll content, nitrogen concentration, and leaf shape factors, whereas native species instead maintained stability with conservative traits such as low specific leaf area. By framing species differences in terms of trait network topology, this study provides mechanistic insight into how introduced *S. apetala* attained competitive dominance and how that dominance could alter the ecosystem's functional structure. Our findings have direct implications for restoration and management: practitioners should weigh the short-term revegetation benefits of *S. apetala* against longer-term risks to native functional diversity and consider restoration designs that promote trait diversity to safeguard ecosystem resilience. Further work should link FTN patterns to demographic performance and site-level environmental gradients to refine management guidance.

Key words: Ecological adaptation, introduced species, leaf functional trait network, mangrove forests, modular analysis, node importance, native species

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Introduction

Mangrove ecosystems are tide-influenced coastal forests dominated by salt-tolerant woody plants in tropical and subtropical regions (Duke et al. 2007). As key blue carbon ecosystems that capture CO_2 and store it long term (especially in waterlogged sediments), they provide critical carbon sequestration, climate

regulation, coastal protection, and biodiversity conservation services (Duke et al. 2007; Solangi et al. 2025). However, under the compounded pressures of anthropogenic disturbance and climate change, approximately 67% of the world's mangroves have been lost or degraded (Li et al. 2025). Although China has only 0.93% of global mangrove area, its mangrove forests are increasingly threatened by habitat fragmentation, declining native species richness, and the erosion of ecological functions (Global Mangrove Alliance 2022). To counter these trends, the fast-growing exotic species *Sonneratia apetala* Buch.-Ham., native to India, Bangladesh, Malaysia, Sri Lanka, and other South Asian countries, was introduced in 1980 as a restoration tool (Ren et al. 2009). Owing to its strong salt tolerance and rapid growth, *S. apetala* has established extensive monospecific stands along the southeastern coasts of China (Wang and Gu 2021), markedly increasing vegetation cover and ecosystem functions in the short term (Chen et al. 2008). However, with its pronounced competitive advantage, *S. apetala* can suppress native mangrove regeneration (Rosas-Guerrero et al. 2025), reduce species composition and functional diversity, and ultimately threaten ecosystem stability (Roscher 2025; Holland et al. 2025). This dynamic exemplifies the "double-edged sword" of ecological restoration, where immediate recovery benefits may be offset by long-term ecological risks (Verleye et al. 2025).

Deciphering the adaptive strategies of *S. apetala* is thus essential for assessing its long-term ecological risks and refining its management. Plant functional traits are widely recognized as fundamental indicators of resource acquisition and environmental adaptability (Pérez-Harguindeguy et al. 2013; Michel et al. 2012; Wright et al. 2017). Although individual traits are relatively stable, they can also be plastic under shifting environmental conditions, and their variation across hierarchical levels, from organs and species to communities and ecosystems, can reveal adaptive strategies (He et al. 2020; Wang et al. 2025). Functional traits, such as specific leaf area, leaf dry matter content and chlorophyll content, are inherently multifunctional, and a single trait often has diverse ecological and physiological functions and therefore requires coordination among multiple traits, tissues, or organs (He et al. 2019). Consequently, examining multiple traits is indispensable for understanding plant ecological strategies. However, empirical studies often rely on dimensionality reduction techniques such as principal component analysis to integrate correlated traits into a few composite axes (Michel et al. 2012; Li et al. 2021; Carmona et al. 2021). Although convenient, such methods risk obscuring the latent multidimensional synergies and interactive relations among traits, thereby masking the integrated adaptive strategies of plants (He et al. 2020).

To overcome these limitations, He et al. (2020) pioneered the application of complex network theory to plant functional ecology, introducing the concept of the functional trait network (FTN). Within this framework, traits are represented as nodes and their interrelations as edges, allowing network topology and node attributes to be used in disentangling adaptive strategies that develop from multi-trait coordination (He et al. 2020; Li et al. 2021; Ye et al. 2024). Trait network analysis not only visualizes nonlinear and asymmetric trait relations but also identifies clusters of strongly correlated traits as integrated "functional modules" (He et al. 2020; Li et al. 2024). High network density reflects tight trait coordination in resource acquisition, conferring a competitive advantage under

resource-limited conditions (Biggs et al. 2020). Likewise, network modularity indicates the functional differentiation of resource-use strategies, while centrality highlights key ecological traits with disproportionate influence on plant performance (Biggs et al. 2020; Choudhary et al. 2024). Thus, FTN analysis is a powerful theoretical tool to elucidate mechanisms of multi-trait coordination, ecological strategies, and niche differentiation.

Recent applications of FTN have yielded important insights across ecosystems such as salt marshes (Ye et al. 2024), arid landscapes (Wang et al. 2023), and tropical rainforests (Buzzard et al. 2016). Compared with leaf and root economics spectra, which rely on linear trade-offs along a single resource axis, FTN integrates modularity, clustering, and centrality to capture nonlinear, multidimensional relations among traits, thereby advancing understanding of plant adaptive strategies in complex environments (He et al. 2020; Li et al. 2021). Despite its promise, the application of FTN to mangrove ecosystems remains limited, and comparative analyses of native mangroves versus the introduced *S. apetala* are virtually absent. Previous studies have primarily examined a narrow set of leaf traits. For instance, *S. apetala* has faster growth and higher photosynthetic efficiency than native species such as *Aegiceras corniculatum* (L.) Blanco and *Avicennia marina* (Forsk.) Vierh. (Wang and Gu 2021), and it leverages larger leaf area and higher foliar nitrogen content to secure a competitive advantage under high light conditions, thereby suppressing native species regeneration (Rosas-Guerrero et al. 2025). However, such analyses, confined to single traits or simple combinations, cannot fully capture the complex adaptive mechanisms operating in natural ecosystems. A critical, unresolved question is how *S. apetala* constructs complex trait networks to consolidate its competitive dominance over native mangroves when a broader suite of traits is considered (Huang et al. 2022).

To answer this question, we investigated five representative native mangrove species in China (*Av. marina*, *Ae. corniculatum*, *Bruguiera gymnorrhiza* (L.) Savigny, *Kandelia obovata* Sheue et al., and *Rhizophora stylosa* Griff.) alongside the introduced mangrove *S. apetala*. We measured leaf-level functional traits and analyzed them using a multidimensional FTN framework. We hypothesized the following: (1) *S. apetala* and native mangrove species differ markedly in the topological properties of their leaf trait networks, with *S. apetala* exhibiting higher connectivity and centralization, indicative of increased resource-use efficiency; and (2) the key trait nodes underpinning network structure also diverge, with native species relying on conservative traits (e.g., lower specific leaf area) to maintain stability, whereas *S. apetala* capitalizes on acquisitive traits (e.g., higher chlorophyll and nitrogen content) to optimize growth and reproduction. In contrast to previous mangrove studies that focus on single traits, FTN retains pairwise trait linkages and quantifies the network-level organization and node roles. Therefore, this framework enables us to move from describing the traits that differ to diagnosing how traits are coordinated and organized as the mechanistic basis for resource-use strategies and potential stability trade-offs. Testing these hypotheses will provide critical insights into the invasion mechanisms of *S. apetala*, enrich our understanding of the multidimensional adaptive strategies of mangroves, and offer theoretical guidance for evidence-based introduction and restoration management.

Methods

Study area overview

The study was conducted along the coastal region of the Beibu Gulf in southern China (21°26'10"–21°52'49"N, 108°14'01"–109°45'45"E), encompassing mangrove ecosystems in Beihai, Qinzhou, and Fangchenggang. Six representative sites were selected as typical mangrove stands along the Guangxi coast based on their relatively intact community structure and species composition, good conservation status with minimal disturbance, and strong nativeness (i.e., well-preserved stands dominated by native mangrove communities). The six sites were as follows: Zhulin (ZL), Yingluowan (YLW), Tieshangang (TSG), and Muan (MA) in Beihai; Kangxiling (KXL) in Qinzhou; and Zhenzhuwan (ZZW) in Fangchenggang (Fig. 1). The region has a subtropical monsoon climate, with a mean annual temperature of 22.9 °C, ranging from 14.2 °C in January to 28.5 °C in July. Annual precipitation varies from 1600 to 2800 mm, with over 70% concentrated between June and August, producing hot, humid summers and mild, dry winters (Chen 2018).

Mangrove forests in the study area are primarily composed of native mangrove species belonging to several families, including *Av. marina* (Acanthaceae); three rhizophoraceous taxa, *B. gymnorrhiza*, *R. stylosa*, and *K. obovata* (Rhizophoraceae); and *Ae. corniculatum* (Primulaceae). In addition, the mangrove community includes the introduced species *S. apetala* (Lythraceae). Collectively, these taxa constitute the characteristic mangrove assemblages of Guangxi Province. The mean community height is approximately 2.48 m (Pan et al. 2024), and soils are classified primarily as coastal saline marsh soils. The tidal regime is diurnal, with a single inundation event per day lasting 6–8 h. Mean annual tidal ranges span 2.2–2.8 m, with maximum differences reaching up to 5.1 m (Chen 2018).

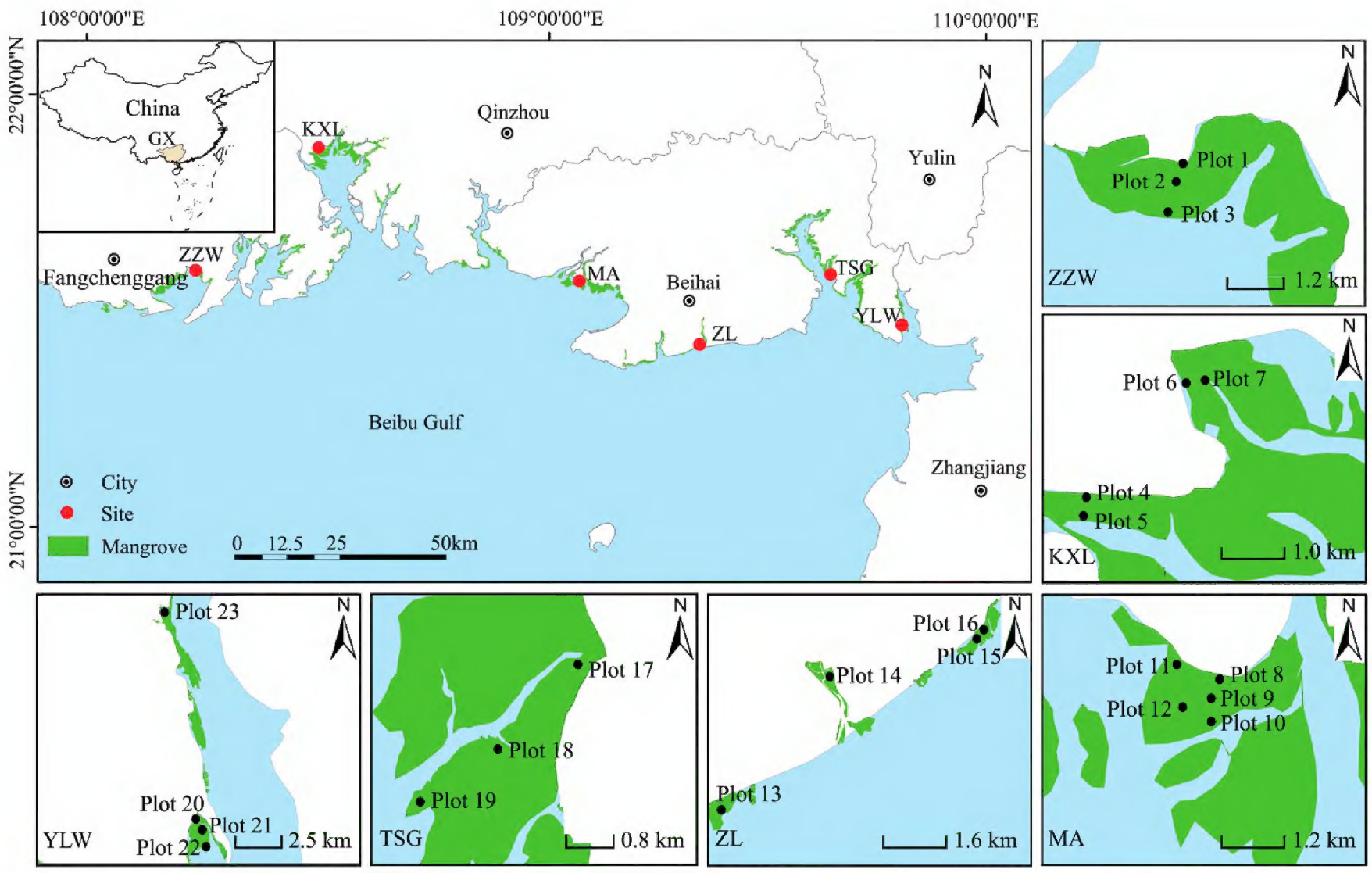

Figure 1. Distribution of different mangrove forest sampling points along the Guangxi coastal area in China. GX, Guangxi; ZZW, Zhenzhuwan; KXL, Kangxiling; MA, Muan; ZL, Zhulin; TSG, Tieshangang; YLW, Yingluowan.

Plot establishment and community survey

Between November and December 2023, we employed a stratified random sampling design to establish permanent plots in representative mangrove stands, with strata defined by tidal elevation (i.e., inundation duration) and spatial distribution. Specifically, the mangrove area at each site was delineated into three tidal-elevation strata: high tide (3–4 h of inundation), mid tide (6–7 h), and low tide (8–9 h). Within each stratum, candidate plot locations were identified in the accessible mangrove area, and plot centers were selected at random from these candidates to avoid subjective placement; if a selected location was unsuitable, it was replaced by another randomly drawn candidate. Each plot measured 10 m × 10 m, yielding 23 plots across the three tidal-elevation strata. Specifically, nine plots were established at high-tide sites, four at mid-tide sites, and ten at low-tide sites. Among these, four plots were established in each of ZL, YLW, and KXL; three in TSG and ZZW; and five in MA. The number of plots per site was adjusted based on local mangrove coverage, species composition, and successional stage to ensure representativeness and capture regional variability. The unequal distribution of plots across tidal elevations reflects the typical zonation pattern of mangroves, in which the lateral extent is more pronounced in high- and low-tide zones but relatively narrow at mid-tide levels.

Vegetation surveys were conducted using the point-centered quarter method. All individuals with basal diameter ≥ 1 cm were recorded, and species identity, basal diameter, diameter at breast height (DBH), tree height, and crown width were measured. In addition, the density and number of seedlings in the regeneration layer and seawater salinity within each plot were systematically documented. Basic information for each plot is summarized in Suppl. material 1.

Sampling and measurement methods for leaf functional traits

Leaf sampling and trait determination followed the standardized functional trait protocols proposed by Pérez-Harguindeguy et al. (2013). We quantified 17 leaf traits that were selected a priori to reflect complementary dimensions of mangrove leaf function relevant to resource-use strategies and stress tolerance. Specifically, the trait set covered the following: (i) morphological/size–geometry traits (e.g., leaf area, leaf length, leaf width, leaf circumference, leaf length/leaf width, leaf petiole area, leaf shape factor and leaf shape coefficient), which reflect canopy light interception and spatial deployment; (ii) structural investment traits (e.g., leaf thickness, leaf dry matter content, and specific leaf area), which relate to construction cost and conservative vs. acquisitive strategies; and (iii) physiological/nutritional traits (e.g., chlorophyll content, chlorophyll reference value, leaf red component, leaf green component, leaf blue component, and leaf nitrogen content), which represent the photosynthetic capacity and nutrient acquisition. In addition, RGB spectral components and a chlorophyll reference value were included as rapid, non-destructive optical descriptors linked to pigment-related variation.

As the mangrove stands were extremely dense (200 stems per 10 × 10 m plot on average) and trait sampling was logistically demanding, we targeted a limited number of representative mature individuals in each plot. Specifically, we selected up to three individuals with intact canopies and no signs of pest damage or disease whose DBH fell within the intermediate size class (i.e., close to the plot median). This strategy reduced potential ontogenetic effects and captured the plot-level

average condition; moreover, community survey data indicated that individuals within the same plot/site had broadly similar heights with no obvious vertical stratification. If fewer than three suitable individuals were available, all individuals were sampled. To avoid directional bias, the canopy of each tree was divided into four quadrants (east, south, west, and north), and leaves were collected evenly from each orientation. From each quadrant, 20 fully expanded, healthy, mature leaves were sampled, yielding 80 leaves per tree. Sampling avoided both the canopy apex and base to ensure that leaves originated from the mid-canopy, where light exposure is relatively uniform. All samples were sealed in labeled plastic bags, stored in portable coolers at low temperature, and transported to the laboratory for subsequent analyses. In total, 7,419 leaves from 93 individuals were collected.

For trait measurements, each leaf was scanned using a leaf area analysis system (YMJ-PC, Zhejiang Top Cloud-agri Technology Co., Ltd, Zhejiang, China) to determine leaf area, leaf petiole area, leaf circumference, spectral components (red, green, and blue), leaf shape factor, leaf shape coefficient, chlorophyll reference value, leaf length, leaf width, and leaf length/leaf width. Chlorophyll content and leaf nitrogen content were measured using a portable chlorophyll meter (FK-YL03, Shandong Fangke Instruments Co., Ltd., Shandong, China). Leaf thickness was determined with a digital caliper (model: LY002F150, precision: 0.01 mm, Deqing Shengtai Core Electronic Technology Co., Ltd., China). Fresh leaf mass was measured with an analytical balance (model: FA224TC, precision: 0.0001 g, Lichen Technology, Shanghai, China), after which leaves were oven-dried at 80 °C to constant weight to obtain dry mass. Derived traits included leaf dry matter content (LDMC = leaf dry mass [g] / fresh mass [g]) and specific leaf area (SLA = leaf area [cm^2] / dry mass [g]).

Statistical analyses

Patterns of variation in mangrove leaf traits

All trait values used for subsequent analyses were summarized at the individual level (n = 93). The normality of each trait was determined using the Shapiro–Wilk test. Subsequently, analyses were conducted only on data conforming to a normal distribution; however, data that did not meet this criterion were log-transformed to approximate normality. Descriptive statistics (mean, minimum, maximum, and coefficient of variation, CV = SD/mean × 100%) were computed to summarize the central tendency and variability.

Analysis of network modularity

To elucidate the network structure and intricate relations among leaf traits, we used network analysis, which is a methodological framework designed to explore the interactions (edges) among entities (nodes) within complex systems (He et al. 2020; Ye et al. 2024). By representing such systems with nodes and edges, network analysis offers a powerful means of simplifying complexity, enabling the structured and quantitative investigation of system architecture and functionality.

We first constructed a correlation matrix (R) among leaf traits, where each element R_{ij} denotes the Pearson correlation coefficient between trait i and trait j. The Pearson correlation coefficient ranges from −1 to 1 and is calculated as follows (Rao et al. 2023; Yang et al. 2025):

$$R_{ij} = \frac{\sum_{k=1}^{n} (x_{ik} - \overline{x_i})(x_{jk} - \overline{x_j})}{\sqrt{\sum_{k=1}^{n} (x_{ik} - \overline{x_i})^2 \sum_{k=1}^{n} (x_{jk} - \overline{x_j})^2}} \quad (1)$$

where x_{ik} represents the value of trait i in sample k, $\overline{x}_i$ is the mean value of trait i, and n denotes the sample size. A positive R_{ij} indicates a positive correlation, with larger values signifying stronger associations; a negative R_{ij} reflects a negative correlation; and $R_{ij} = 0$ suggests no correlation.

The full correlation matrix captures all pairwise relations and thus directly converting it into a network would result in an excessively dense and complex structure. To address this problem, we imposed a threshold and retained only those relations with $|R_{ij}| > 0.2$ and significance at $p < 0.05$ (Dormann et al. 2010; Gao et al. 2022). Only trait pairs surpassing this threshold were retained as edges in a network.

We used the filtered correlations to construct an undirected, weighted network of leaf traits, where each node represented a distinct leaf trait and edge weights corresponded to the strength of correlation. The network was represented by an adjacency matrix (A), defined as follows:

$$A_{ij} = \begin{cases} |R_{ij}|, \text{if} & |R_{ij}| > 0.2 \\ 0, & \text{otherwise} \end{cases} \quad (2)$$

where A_{ij} denotes the weight of the edge between node i and node j; if $A_{ij} = 0$, no direct connection exists between the two nodes under the threshold criterion.

Subsequently, we partitioned the network into modules using the Louvain algorithm, as implemented in the igraph package in R v4.3.1. The quality of modularity partitioning was evaluated using the modularity index (Q), calculated as follows:

$$Q = \frac{1}{2n} \sum_{ij} \left(A_{ij} - \frac{k_i k_j}{2m} \right) \delta(c_i, c_j) \quad (3)$$

where m is the sum of all edge weights in the network; k_i and k_j are the weighted degrees of nodes i and j, respectively, and $\delta(c_i, c_j)$ is an indicator function that equals 1 if nodes i and j belong to the same module and 0 otherwise. The value of Q typically ranges between −0.5 and 1, with higher values indicating more distinct modular structures. Last, the network was visualized using the ggraph package in R.

Comparison of overall network parameters

Global network parameters are critical for characterizing network fundamental structural properties (He et al. 2020; Li et al. 2021). The principal metrics considered were edge density (D), average path length (L), network diameter (D_{max}), average clustering coefficient (C), and modularity (Q), defined as follows:

$$D = \frac{2E}{N(N-1)} \quad (4)$$

$$L = \frac{1}{\frac{N(N-1)}{2}} \sum_{i \neq j} d(i,j) \quad (5)$$

$$C_i = \frac{2T_j}{k_i\,(\mathrm{k_i}-1)} \tag{6}$$

where E denotes the number of edges and N the number of nodes in the network. D quantifies the overall connectivity of the network, with higher values indicating a more densely connected structure. $d(i, j)$ represents the shortest path length between nodes i and j. Hence, a smaller L reflects a more compact and efficiently connected network architecture. T_i denotes the number of triangles formed around node i, and k_i represents the degree of node i. C_i captures the tendency of nodes to form tightly knit groups, offering insight into the local cohesion of the network.

Comparison of network node parameters

To assess the importance and positional roles of individual leaf traits within the network, we quantified the significance of each trait using a suite of node-level parameters, including degree, closeness centrality, betweenness centrality, and clustering coefficient. Node-level metrics were computed from the final trait–network adjacency matrix. Shortest path-based metrics were calculated using geodesic distances and betweenness was normalized by the theoretical maximum. The clustering coefficient was estimated as the local clustering of each node (Dormann et al. 2010; Gao et al. 2022). Degree denotes the number of edges linked to a node, reflecting its direct interactions and potential influence within the network. Closeness centrality quantifies a node's average shortest-path distance to all other nodes, enabling rapid information dissemination due to its central proximity. Betweenness centrality measures how frequently a node occupies shortest paths between pairs of other nodes, positioning it as a bridge that controls inter-cluster communication. Notably, closeness centrality prioritizes overall proximity, whereas betweenness centrality emphasizes the role of bridging distant network segments. The metrics were defined as follows:

$$C(i) = \frac{N-1}{\sum_{j\neq i} d(i,j)} \tag{7}$$

$$B(i) = \sum_{s\neq i\neq t} \frac{\sigma_{st}(i)}{\sigma_{st}} \tag{8}$$

$$C(ci) = \frac{2T_{(i)}}{k_{(i)}\left[k_{(i)^{-1}}\right]} \tag{9}$$

where $C_{(i)}$ represents the reciprocal of the average shortest path length from node i to all other nodes; $\sigma_s t$ denotes the total number of shortest paths between nodes s and t, while $\sigma_{st}(i)$ is the number of those paths that pass through node i; $B(i)$ thus measures the frequency with which node i lies along the shortest paths connecting other node pairs; $T(i)$ represents the number of triangles involving node (i), $k_{(i)}$ is the degree of node (i), $C_{(ci)}$ captures the density of connections among the immediate neighbors of node i.

Relations between network node parameters and stability

To gain a deeper understanding of the functional roles of leaf traits within the network structure, as well as their ecological significance and adaptive capacity, we performed linear regression analyses between node-level parameters

and trait stability and visualized the relations using scatter plots. With this approach, we examined the trends in how each node-level parameter varied with trait stability. The strength and significance of these relations were evaluated based on the coefficient of determination (R^2) and the p-value. Here, R^2 represents the proportion of the variance in the dependent variable that can be explained by the independent variable through the regression model, serving as an indicator of model goodness-of-fit. The *p*-value, representing the probability level, is used to assess the significance of the regression. Consequently, results with $p < 0.05$ were considered significant, with smaller *p*-values indicating stronger evidence against the null hypothesis.

All statistical analyses and visualizations were conducted in R v4.3.1, using the packages igraph, dplyr, tidygraph, and ggplot2.

Results

Fundamental mangrove leaf traits

Leaf trait values of native mangrove species were generally greater than those of the introduced species. Notably, the mean values of leaf circumference, chlorophyll reference value, leaf length, leaf length/leaf width, leaf nitrogen content, and chlorophyll content were higher in the introduced species than in native mangrove species, whereas all other leaf trait means were greater in native mangrove species (Table 1). Furthermore, the range of leaf trait values was broader in native mangrove species than in the introduced species (Table 1). Except for leaf green component, leaf shape factor, and leaf length/leaf width, the coefficients of variation for leaf traits were consistently higher in native mangrove species than in the introduced species (Table 1).

Table 1. Descriptive statistics of mangrove leaf traits.

Trait	Unit	Mean	Min-Max	(CV%)
Leaf petiole area, LPA	cm^2	0.29 [0.20]	0.00–8.19 [0.00–0.53]	1.09 [0.70]
Leaf circumference, LC	cm	17.54 [19.27]	7.13–32.21 [11.38–30.30]	0.30 [0.15]
Leaf red component, LRC	%	13.89 [4.69]	1.00–96.00 [1.00–23.00]	0.81 [0.71]
Leaf green component, LGC	%	28.55 [10.08]	1.00–119.00 [2.00–39.00]	0.62 [0.69]
Leaf blue component, LBC	%	6.59 [5.32]	1.00–53.00 [2.00–21.00]	0.75 [0.57]
Leaf shape factor, LSF	/	0.75 [0.53]	0.08–0.97 [0.32–0.82]	0.12 [0.17]
Leaf shape coefficient, LSC	/	0.70 [0.67]	0.24–0.82 [0.59–0.76]	0.05 [0.05]
Chlorophyll reference value, ChlV	/	1.81 [3.50]	0.86–12.53 [1.36–6.59]	0.62 [0.31]
Leaf area, LA	cm^2	18.96 [15.34]	2.71–76.45 [8.13–24.90]	0.56 [0.22]
Leaf length, LL	cm	7.26 [8.65]	2.34–21.07 [4.62–12.51]	0.34 [0.16]
Leaf width, LW	cm	3.57 [2.65]	1.48–9.24 [1.82–3.65]	0.25 [0.13]
Leaf length/Leaf width, L/W	cm/cm	2.03 [2.29]	0.37–4.93 [1.84–3.11]	0.21 [5.35]
Leaf nitrogen content, LNC	mg/g	18.51 [21.77]	0.24–32.05 [16.26–26.61]	0.19 [0.07]
Leaf thickness, LT	mm	0.42 [0.35]	0.02–1.69 [0.12–0.70]	0.37 [0.21]
Chlorophyll content, Chl	SPAD	50.26 [60.33]	2.92–92.70 [42.89–75.58]	0.21 [0.08]
Specific leaf area, SLA	cm^2/g	74.12 [69.45]	2.27–605.00 [38.02–165.58]	0.35 [0.18]
Leaf dry matter content, LDMC	g/g	0.31 [0.28]	0.01–0.62 [0.14–0.68]	0.89 [0.14]

Values outside brackets denote native mangroves; values within brackets denote introduced *S. apetala*.

Comparative network analysis of leaf traits in native and introduced mangrove species

According to the results derived from the Louvain algorithm, the 17 leaf traits of native mangrove species were partitioned into three distinct communities or modules. The first community comprised nine traits: leaf red component, leaf blue component, chlorophyll content, leaf nitrogen content, leaf green component, leaf petiole area, chlorophyll reference value, leaf area, and leaf width. The second community included six traits: leaf thickness, leaf circumference, leaf length, leaf length/leaf width, leaf shape factor, and leaf shape coefficient. The third community consisted of two traits: specific leaf area and leaf dry matter content (Fig. 2A). By contrast, the 17 leaf traits of *S. apetala* were clustered into two communities. The first community encompassed ten traits: chlorophyll content, leaf nitrogen content, leaf petiole area, leaf shape factor, leaf shape coefficient, leaf length/leaf width, leaf length, leaf width, leaf circumference, and leaf area. The second community comprised seven traits: leaf thickness, chlorophyll reference value, specific leaf area, leaf dry matter content, leaf red component, leaf blue component, and leaf green component (Fig. 2B).

Within the global parameters of leaf trait networks, edge density was higher for the introduced species than for native mangroves, whereas average path length, network diameter, and mean clustering coefficient were consistently greater for native species than for the introduced species (Fig. 3).

The correlations among node connections and their corresponding degrees are illustrated in Fig. 4. Specifically, the edge weights of native mangrove species were

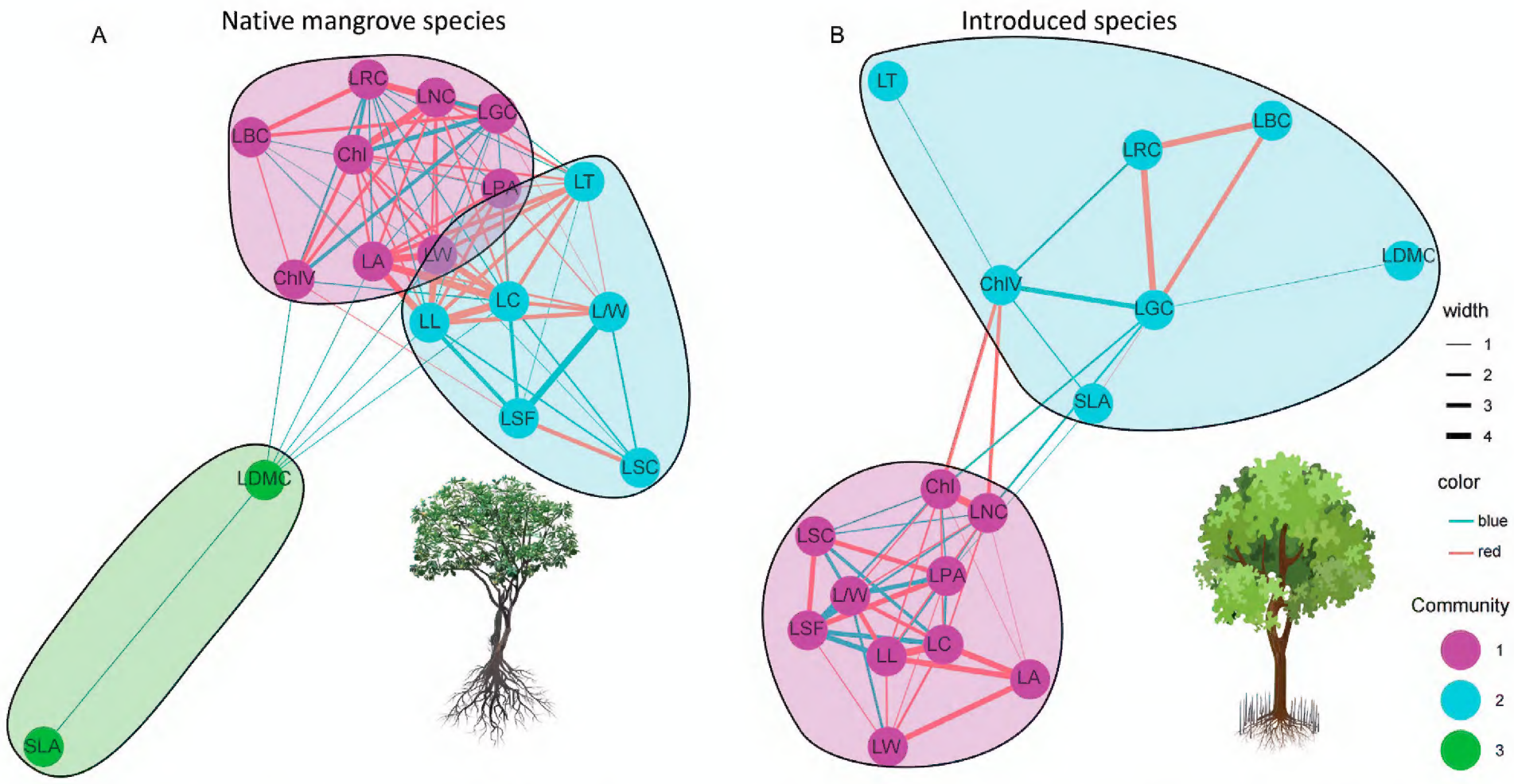

Figure 2. Leaf trait network diagram of **A.** Native mangrove species and **B.** The introduced species *S. apetala* in mangrove forests of southern coastal China. LPA, leaf petiole area; LC, leaf circumference; LRC, leaf red component; LGC, leaf green component; LBC, leaf blue component; LSF, leaf shape factor; LSC, leaf shape coefficient; ChlV, chlorophyll reference value; LA, leaf area; LL, leaf length; LW, leaf width; L/W, leaf length/leaf width; LNC, leaf nitrogen content; LT, leaf thickness; Chl, chlorophyll content; SLA, specific leaf area; LDMC, leaf dry matter content. Line thickness indicates the strength of correlations among traits, with red representing positive correlations and blue representing negative correlations.

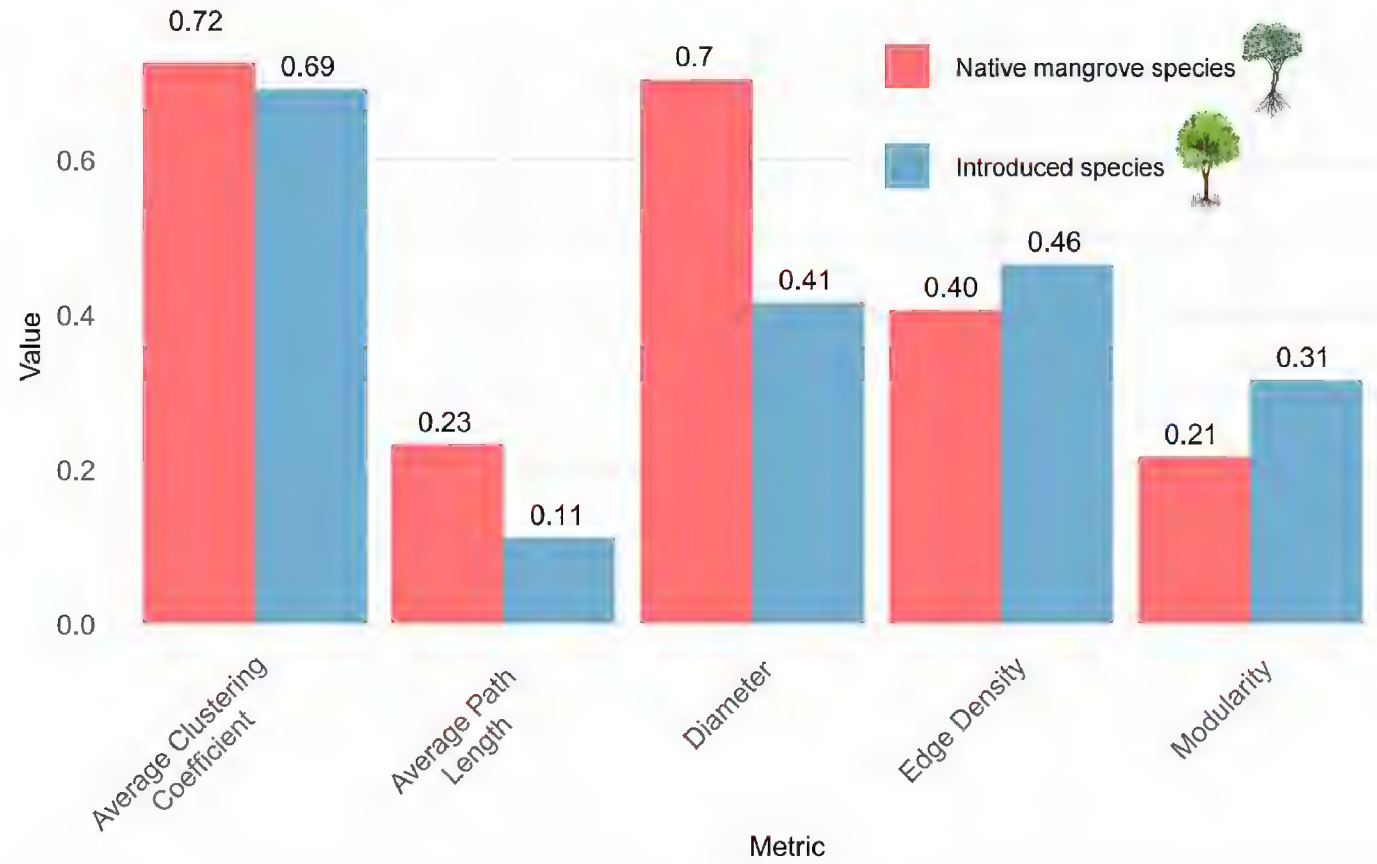

Figure 3. Trait network variation between native mangroves species and the introduced species *S. apetala* in mangrove forests of southern coastal China.

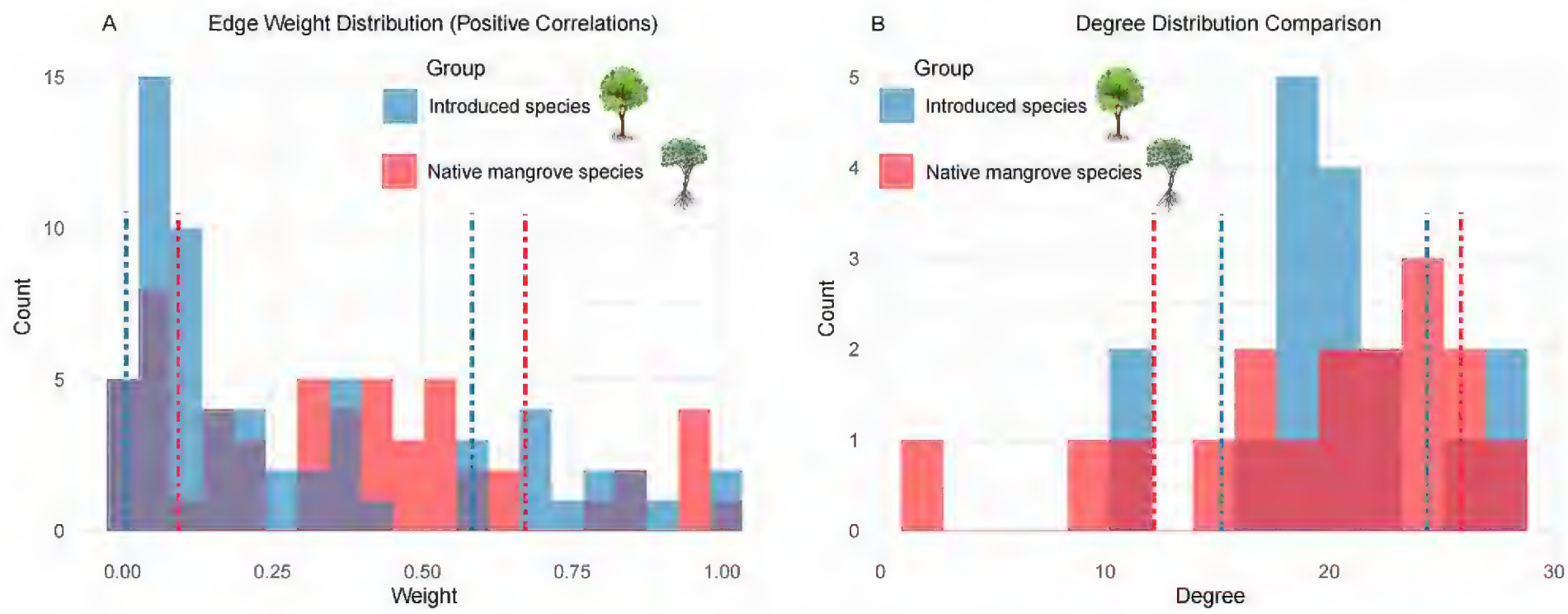

Figure 4. A) Edge weight distribution and B) degree distribution in the leaf trait network of native mangroves species and the introduced species *S. apetala* in mangrove forests of southern coastal China.

predominantly distributed between 0.10 and 0.65, whereas those of the introduced species were concentrated within a slightly wider range of 0.00 to 0.57 (Fig. 4A). For degree distribution, individual nodes in native species were primarily connected within the range of 12 to 27 edges, while the distribution of the introduced species was more constrained and largely confined to 16 to 25 edges (Fig. 4B).

Comparison of network node parameters of leaf traits between native and introduced mangrove species

The network parameters of native and introduced mangrove species are presented in Fig. 5. For native species, leaf length, leaf area, and leaf circumference exhibited relatively high degree and closeness centrality, whereas the introduced species was characterized by elevated values of chlorophyll content, leaf nitrogen content, and

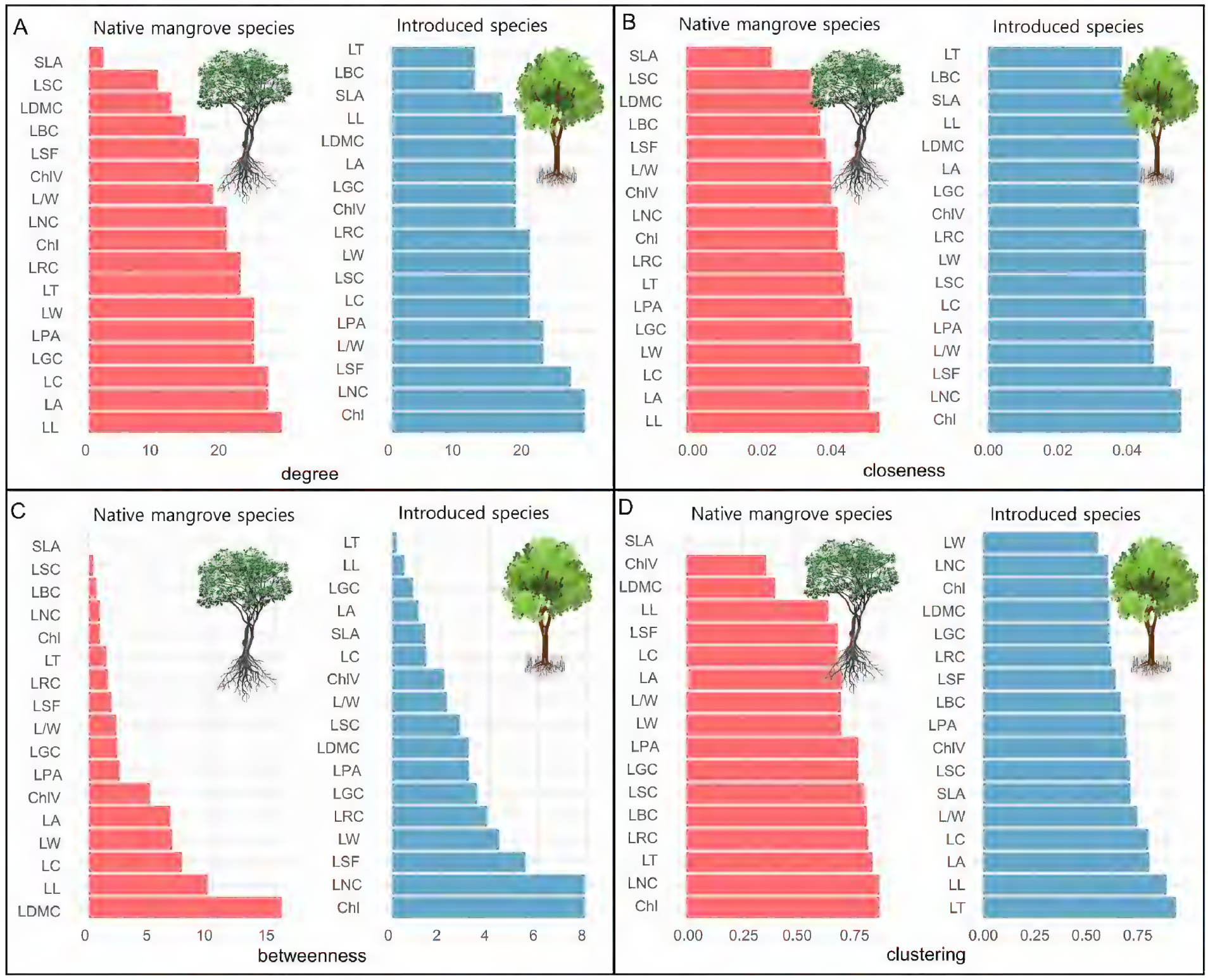

Figure 5. Comparison of the node parameters **A.** degree; **B.** closeness; **C.** betweenness, and **D.** clustering of the leaf trait network between native mangrove species and the introduced species *S. apetala* in mangrove forests of southern coastal China. LPA, leaf petiole area; LC, leaf circumference; LRC, leaf red component; LGC, leaf green component; LBC, leaf blue component; LSF, leaf shape factor; LSC, leaf shape coefficient; ChlV, chlorophyll reference value; LA, leaf area; LL, leaf length; LW, leaf width; L/W, leaf length/leaf width; LNC, leaf nitrogen content; LT, leaf thickness; Chl, chlorophyll content; SLA, specific leaf area; LDMC, leaf dry matter content.

leaf shape factor for these same metrics (Fig. 5A, B). With respect to betweenness centrality, native species attained the highest values in leaf dry matter content, while the introduced species was predominantly associated with chlorophyll and nitrogen contents (Fig. 5C). For the clustering coefficient, chlorophyll and nitrogen contents were more pronounced in native species, whereas leaf thickness and leaf length were the dominant traits for the introduced species (Fig. 5D). Collectively, these findings indicated that native mangrove species tended to rely on conservative traits, such as lower specific leaf area, to sustain community stability, while the introduced species exploited core functional traits, including high chlorophyll leaf nitrogen contents and leaf shape factor, to develop a highly efficient and tightly integrated resource-use strategy.

Both native and introduced mangrove species exhibited a significant positive linear relation between node degree and strength (native: R^2 = 0.86 [Fig. 6A]; introduced: R^2 = 0.56 [Fig. 6B]), although the association was markedly stronger in native than in the introduced species (Fig. 6).

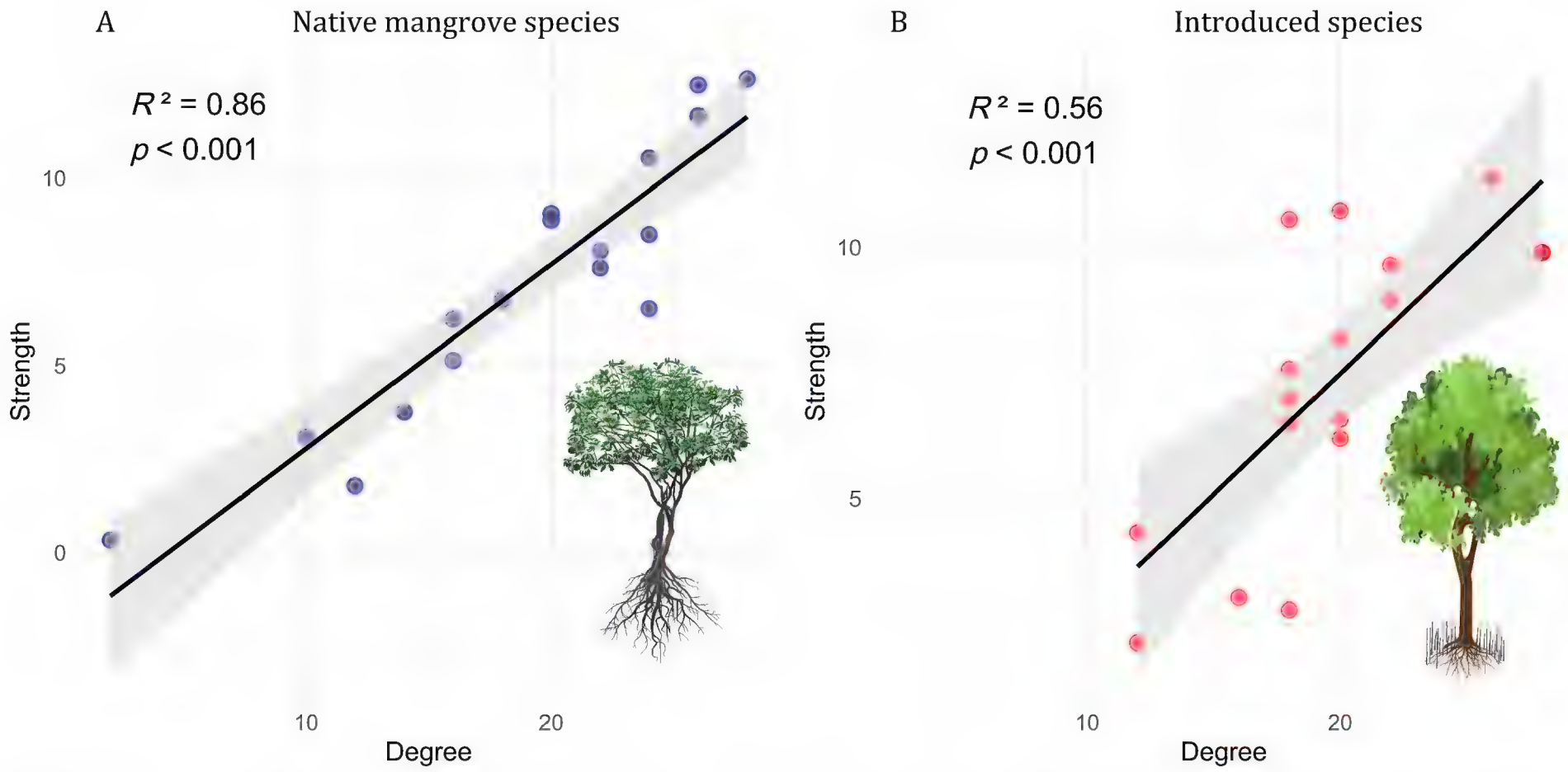

Figure 6. Linear regression of the node degree–strength of correlation in leaf trait networks of **A.** Native mangrove species and **B.** The introduced species *S. apetala* in mangrove forests of southern coastal China. Regression lines are shown with 95% confidence intervals (shaded areas). R^2 represents the coefficient of determination, indicating the proportion of variance in strength explained by degree.

Relations between network node parameters and trait stability in native and introduced mangrove species

Relations between leaf trait network parameters and stability are illustrated in Fig. 7. In native mangrove species, both degree and closeness centrality were significantly and positively related to stability ($p < 0.05$), whereas in the introduced species, the same relations were slightly negative and not significant ($p > 0.05$) (Fig. 7A, B). The betweenness centrality of the introduced species was significantly negatively related to stability ($p < 0.05$), while the clustering coefficient was significantly positively related ($p < 0.05$). In native species, although both betweenness centrality and clustering coefficient were positively associated with stability, neither relation was significant ($p > 0.05$) (Fig. 7C, D).

Discussion

Comparative analysis of leaf trait networks between native and introduced mangrove species

In this study, we distinguished between two leaf trait network structures: the centralized-efficient strategy and the dispersed-cooperative strategy. The centralized-efficient strategy was characterized by fewer modules and higher node centrality, facilitating rapid growth in resource-abundant environments but lacking regulatory flexibility under resource constraints. In contrast, the dispersed-cooperative strategy was marked by more modules and greater system redundancy, enhancing adaptability and stability, particularly in dynamic and stress-prone environments.

Network analysis quantifies the synergies and dependencies among various leaf traits, offering a systematic perspective for understanding the mechanisms underlying functional trait integration of plants in ecosystems, particularly under dynamic environmental pressures (He et al. 2020; Li et al. 2024). We found that

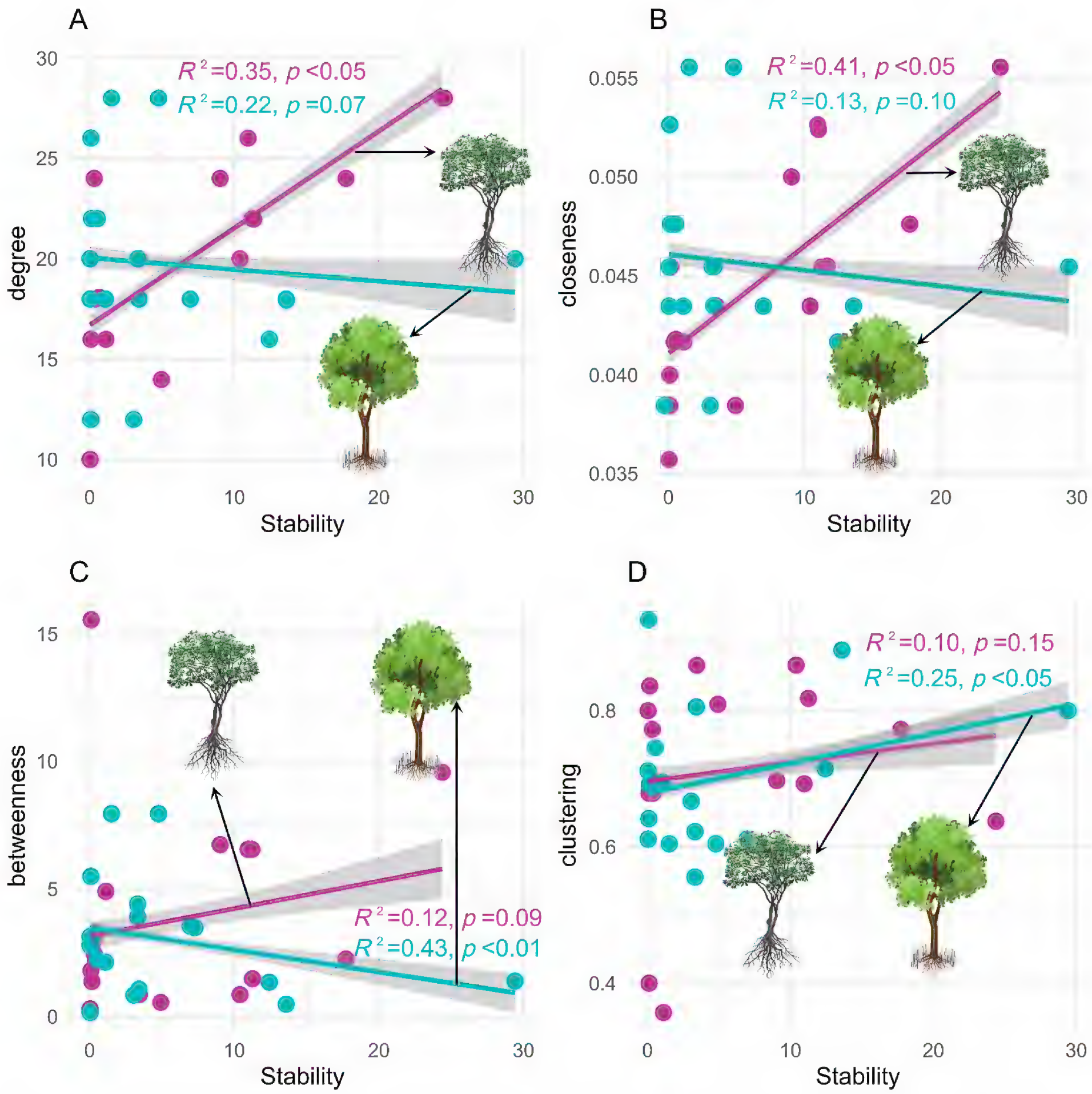

Figure 7. Linear regressions of the relations between the node parameters **A.** Degree; **B.** Closeness; **C.** Betweenness, and **D.** Clustering and stability of leaf trait network of native mangrove species and the introduced species *S. apetala* in mangrove forests of southern coastal China. Regression lines are shown with 95% confidence intervals (shaded areas). R^2 represents the coefficient of determination, indicating the proportion of variance in stability explained by the corresponding node parameter.

native mangrove species assembled a dispersed-cooperative strategy, organized into three functional modules, whereas the introduced species *S. apetala* constructed a centralized-efficiency network structure comprising only two functional modules (Fig. 2). This divergence in modular organization underscores fundamental differences in ecological adaptation strategies and trait integration mechanisms between the two groups. *Sonneratia apetala* is native to tropical South Asia (India to Myanmar, including Bangladesh) and was introduced to southern China from Bangladesh in the 1980s for mangrove restoration (Ren et al. 2009). Although the native and introduced regions are both influenced by monsoonal coastal climates, the introduction sites in Southeast China represent a higher-latitude range margin

where winter chilling/frost events and photoperiod regimes differ from those in the core native range (Wang and Gu 2021). Therefore, the contrasted trait–network architectures likely reflect a combination of pre-adaptation to dynamic estuarine habitats in the native range and rapid acclimation/phenotypic plasticity to novel stress regimes after introduction, rather than requiring long-term co-evolution with local native mangroves (Rosas-Guerrero et al. 2025). During ecological evolution, native mangrove species develop diversified niche differentiation strategies, reflected in their highly modular leaf trait networks. The independent regulation of distinct modules likely increases niche partitioning and confers greater adaptability and stability in heterogeneous environments (Reich and Cornelissen 2014). In contrast, the trait network of the fast-growing pioneer species *S. apetala* contained fewer modules and showed a more centralized organization. Such a structure may offer competitive advantages in resource-abundant environments; however, reduced regulatory flexibility compromises system robustness under resource constraints or intensified environmental stresses (Wang et al. 2020; Li et al. 2024).

The leaf trait network of *S. apetala* exhibited a higher edge density than that of native mangrove species (Fig. 3). Because trait networks are constructed from trait–trait correlations, the network edges and modules primarily reflect patterns of statistical co-variation; therefore, the functional interpretations drawn from these topological features should be regarded as inferential hypotheses rather than direct demonstrations of causal interactions or realized "dominance/efficiency" strategies (He et al. 2020). An elevated edge density has often been interpreted as tighter coordination among subsets of traits, indicating the potential emergence of relatively semi-independent trait syndromes, which may reduce functional redundancy and alleviate internal resource trade-offs (Reich and Cornelissen 2014). For instance, invasive *Spartina alterniflora* achieves rapid expansion through the highly modular organization of tillering and photosynthetic traits (Davidson et al. 2011). In this context, the high modularity observed in *S. apetala* may be consistent with the enhanced potential for rapid and localized responses to environmental stressors through partially decoupled functional units, aligning conceptually with the "phenotypic plasticity first" hypothesis proposed for invasive species (Richards et al. 2006).

Conversely, native mangrove species showed longer average path lengths and higher clustering coefficients than the introduced species (Fig. 3), suggesting a more integrated, "multi-tiered" topology that is often described as small-world-like (Verleye et al. 2025). For example, in *K. obovata*, stomatal conductance and xylem hydraulic conductivity are linked via intermediate traits such as specific leaf area (Yang et al. 2024), forming a coordinated trait chain. Such a complex network architecture increases system capacity to buffer environmental fluctuations, consistent with the "metabolic–ecological stability" theory proposed by Enquist et al. (2015), which posits that trait redundancy and interdependence confer systemic resilience. Although *S. apetala* demonstrates a rapid adjustment capacity through its "centralized efficiency" modular network, its "high-responsiveness, low-buffering" mechanism carries substantial ecological risks. The disruption of critical trait nodes could precipitate systemic collapse. For instance, during the 2008 frost event in Guangxi mangroves, approximately 50% of *S. apetala* leaves in Haikou and Zhanjiang turned yellow, while complete leaf necrosis was observed in Fangchenggang, Guangxi. In contrast, only 30% yellowing was observed in the native *B. gymnorrhiza* (Chen et al. 2010). This disparity with the introduced species likely reflects the greater trait redundancy and stability mechanisms inherent to the native mangrove network structure.

Node parameters of leaf trait networks in native and introduced mangrove species and their implications for stability

In this study, native mangrove species exhibited higher degree and closeness centrality in leaf length, leaf area, and leaf circumference, whereas *S. apetala* exhibited elevated degree and closeness centrality in chlorophyll content, leaf nitrogen content, and leaf shape factor (Fig. 5). This pattern suggests that leaf length, area, and circumference are highly interconnected within the trait network of native mangrove species. Such a structure likely reflects long-term ecological adaptation, whereby stable morphological traits such as expanded leaf area and circumference optimize photosynthetic performance and water-use efficiency across evolutionary timescales (Sobrado 2005). By contrast, the introduced species *S. apetala* exhibits robust growth capacity and pronounced environmental adaptability, particularly by maintaining high chlorophyll and leaf nitrogen contents and a plastic leaf shape factor under varying light conditions. This strategy enables *S. apetala* to rapidly occupy and adapt to new environments via increased photosynthetic rates and nutrient uptake efficiency (Wang et al. 2020). Notably, leaf dry matter content, a critical indicator of leaf structural strength and construction cost (Wright et al. 2004), exhibited high betweenness centrality within native mangrove species. This finding is consistent with observations in typical broad-leaved pine forests, where leaf dry matter content is significantly correlated with multiple functional traits (Xun et al. 2020), underscoring its dual role as an independent functional trait and as a "bridge" linking distinct trait modules. By contrast, *S. apetala* primarily relied on chlorophyll and leaf nitrogen contents to bridge different functional communities, serving as central nodes that integrated distinct modules. As key indicators of photosynthetic capacity and nitrogen-use efficiency (Wright et al. 2004), elevated chlorophyll and nitrogen levels enable *S. apetala* to optimize photosynthesis and nutrient assimilation over short timescales, thus facilitating rapid growth and biomass accumulation in competitive environments. Additionally, native mangrove species exhibited higher clustering coefficients for chlorophyll and leaf nitrogen contents, whereas *S. apetala* showed higher clustering coefficients for leaf thickness and leaf length (Fig. 5). Previous studies (Ball 1988; Feller et al. 2007) emphasize that nitrogen is essential for the synthesis of photosynthetic enzymes (e.g., Rubisco) and chlorophyll. Therefore, relatively high chlorophyll and nitrogen contents are crucial for native mangrove species to efficiently capture light energy in intertidal habitats, reflecting a conservative resource-use strategy shaped by prolonged exposure to high salinity, anoxic soils, and periodic tidal stresses. In contrast, the relatively high clustering of leaf thickness and leaf length in *S. apetala* suggests that these morphological traits form a tightly coordinated local trait syndrome. Such coordination may be consistent with enhanced structural investment and/or morphological plasticity, which could improve resource acquisition or stress tolerance and hypothetically contribute to competitive advantages over native species under certain conditions (Guarino et al. 2021; Casares et al. 2025). However, these implications should be viewed as potential consequences inferred from trait co-variation rather than direct evidence of competitive exclusion.

In the trait networks of native mangrove species, both degree and closeness centrality were significantly positively related to trait stability (Fig. 7). In long-established native mangroves, highly central traits are repeatedly filtered by chronic intertidal stressors and thus tend to be constrained by stabilizing selection and

developmental canalization, resulting in lower variability (Wang and Gu 2021). In contrast, in introduced *S. apetala*, centrality is concentrated in fast-response physiological traits that are inherently plastic and sensitive to fluctuating resources at the introduction range margin, leading to higher within-species variability (Ren et al. 2009). In this case, strong trait–trait covariation may reflect shared plastic responses to environmental heterogeneity rather than canalized, long-term trait integration. This pattern likely develops from the evolutionary history of mangroves, wherein complex, interdependent trait networks evolved through functional diversity and redundancy. Traits with high degree and closeness centrality may be critical for survival in dynamic environments and thus subject to strong stabilizing selection, resulting in reduced variability and increased stability over evolutionary timescales (Walker et al. 2006; Alongi 2008). By contrast, in the introduced species *S. apetala*, relations between degree and closeness centrality and stability of leaf traits were negative, albeit nonsignificant (Fig. 7). This negative association may reflect a more flexible adaptive strategy in novel environments, suggesting that traits with high centrality are relatively unstable, likely due to heightened sensitivity to environmental fluctuations such as resource limitation and light variability (Ren et al. 2009; Funk et al. 2016).

Moreover, the betweenness centrality of *S. apetala* was significantly negatively related to trait stability, whereas in native mangrove species, the relation was positive but nonsignificant (Fig. 7). This contrast suggests that the "bridge traits" in *S. apetala* such as chlorophyll content and leaf nitrogen content had relatively high variability, reflecting a flexible, opportunistic strategy to rapidly exploit ecological niches (Parker et al. 2006; Chen et al. 2008). In native mangrove species, by contrast, bridge traits such as leaf dry matter content had relatively high betweenness centrality with increased stability, enabling the maintenance of robust intermodule connections within the trait network. Such stable bridging traits are crucial for increasing ecosystem resilience and facilitating long-term adaptation to environmental disturbances (Walker et al. 2006; Reich and Cornelissen 2014). In both *S. apetala* and native mangrove species, the clustering coefficient was positively associated with stability, although the relation was only significant for *S. apetala*. Traits in *S. apetala* with high clustering coefficients, notably leaf thickness and leaf length, tended to form tightly knit local trait clusters. These localized trait assemblies may increase stability, allowing the introduced species to rapidly expand through concentrated resource allocation and heightened adaptability (Alongi 2008). By tightly coordinating resource-use traits, *S. apetala* likely mitigates the effects of external environmental variability on individual traits, thereby sustaining relatively high trait stability in novel environments (Funk et al. 2016).

Conclusions and perspectives

We used functional trait network (FTN) analysis to systematically compare the leaf-level network structures and ecological strategies of native mangrove species and the introduced *S. apetala* and found marked divergences in functional organization and resource-use patterns. Native mangrove networks had high modularity and strong cross-module coordination, indicating a "dispersed-cooperative strategy" mode of resource utilization. Thus, because of relative independence and redundancy among traits, native species maintain community stability and ecological resilience under complex and fluctuating environments. By contrast,

S. apetala had a "centralized-efficient" strategy, with networks marked by low modularity and high connectivity. By relying on hub traits such as higher chlorophyll content, nitrogen concentration, and leaf shape factor, *S. apetala* establishes rapid and efficient resource acquisition pathways, enabling swift expansion under resource-rich conditions but potentially constraining its performance under resource scarcity or intensified stress. These distinctions suggest that while *S. apetala* can substantially increase vegetation cover and certain ecosystem functions during early restoration, its "centralized-efficient" strategy may compress the ecological niches of native species and erode functional diversity. Notably, the elevated chlorophyll and nitrogen contents of *S. apetala* not only increase its resource-use efficiency but may also amplify its invasive potential, exerting sustained pressure on native communities. From an applied perspective, our results suggest that the large-scale planting of *S. apetala* should be avoided in or near intact native mangrove stands to reduce long-term risks to native community stability and functional diversity. Where restoration is required, priority should be given to native mangrove species, and *S. apetala*—if used at all—should be restricted to carefully managed, spatially isolated sites with clear containment objectives. In areas where *S. apetala* has already formed dense stands, targeted thinning or gradual replacement with native species may relieve competitive pressure and promote close-to-nature community recovery.

We provide a novel perspective for understanding the functional trait networks and adaptive strategies of mangroves while offering theoretical insights for the management of introduced species. Nonetheless, several limitations remain. First, the networks were constructed solely from leaf-level traits, neglecting stem and root traits that may capture whole-plant coordination in resource allocation and environmental adaptation. Second, although structural differences in networks were identified, their direct coupling with environmental drivers was not examined, limiting the capacity to pinpoint key ecological factors and mechanisms shaping network divergence. Future research should therefore (i) broaden the scope of trait data collection to include stem traits (e.g., wood density, vessel diameter) and root traits (e.g., specific root length, root tissue density, root depth distribution), thereby enabling whole-plant trait network analyses to more comprehensively reveal multidimensional adaptive strategies and (ii) integrate environmental monitoring data such as light availability, soil nutrients, and salinity to investigate the coupling between FTN variation and environmental gradients, thereby clarifying the ecological drivers of mangrove community stability and exotic species invasion. Such efforts will strengthen the empirical basis for evidence-based restoration and management strategies.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Conceptualization: YFP. Formal analysis: YFP, STQ. Investigation: XRT, YFP. Methodology: YFP, XRT. Data curation: XRT, STQ, ZNS, YFP, LHP. Visualization: YFP. Funding acquisition: GLQ, HQF. Writing—original draft: YFP. Writing—review and editing: XRT, YFP, LHP, STQ, ZNS, GLQ, HQF.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

Alongi DM (2008) Mangrove forests: Resilience, protection from tsunamis, and responses to global climate change. Estuarine, Coastal and Shelf Science 76: 1–13. https://doi.org/10.1016/j.ecss.2007.08.024

Ball MC (1988) Salinity tolerance in the mangroves aegiceras corniculatum and avicennia marina. i. water use in relation to growth, carbon partitioning, and salt balance. Functional Plant Biology 15(3): 447–467. https://doi.org/10.1071/PP9880447

Biggs CR, Yeager LA, Bolser DG, Bonsell C, Dichiera AM, Hou Z, Keyser SR, Khursigara AJ, Lu K, Muth AF, Negrete B, Erisman BE (2020) Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. Ecosphere 11(7): e03184. https://doi.org/10.1002/ecs2.3184

Buzzard V, Hulshof CM, Birt T, Violle C, Enquist BJ (2016) Re-growing a tropical dry forest: Functional plant trait composition and community assembly during succession. Functional Ecology 30: 1006–1013. https://doi.org/10.1111/1365-2435.12579

Carmona CP, Bueno CG, Toussaint A, Träger S, Díaz S, Moora M, Munson AD, Pärtel M, Zobel M, Tamme R (2021) Fine-root traits in the global spectrum of plant form and function. Nature 597: 683–687. https://doi.org/10.1038/s41586-021-03871-y

Casares FA, de Melo VR, Loureiro M, Pires-Teixeira LM, Oigman-Pszczol SS, Pszczol E, Creed JC (2025) The Brazilian Biological Invasion Platform: Six years of lessons learned reporting non-native marine species. NeoBiota 103: 231–248. https://doi.org/10.3897/neobiota.103.157105

Chen X (2018) On the construction of Beihai mangrove wetl and ecosystem research station in Guangxi. Shaanxi Forest Science and Technology 46: 107–109. [in Chinese with English abstract]

Chen L, Tam NFY, Huang J, Zeng X, Meng X, Zhong C, Wong Y, Lin G (2008) Comparison of eco-physiological characteristics between introduced and indigenous mangrove species in China. Estuarine, Coastal and Shelf Science 79(4): 644–652. https://doi.org/10.1016/j.ecss.2008.06.003

Chen L, Wang W, Zhang Y, Huang L, Zhao C, Yang S, Yang Z, Chen Y, Xu H, Zhong C, Su B, Fang B, Chen N, Zeng C, Lin G (2010) Damage to mangroves from extreme cold in early 2008 in southern China. Chinese Journal of Plant Ecology 34: 186–194. [in Chinese with English abstract]

Choudhary B, Dhar V, Pawase AS (2024) Blue carbon and the role of mangroves in carbon sequestration: Its mechanisms, estimation, human impacts and conservation strategies for economic incentives. Journal of Sea Research 199: 763–775. https://doi.org/10.1016/j.seares.2024.102504

Davidson AM, Jennions M, Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecology Letters 14(4): 419–431. https://doi.org/10.1111/j.1461-0248.2011.01596.x

Dormann CF, Mcpherson JM, Araújo MB, Bivand R, Bolliger J, Carl G, Davies RG, Hirzel AH, Jetz W, Kissling WD, Kühn I, Ohlemüller R, Peres-Neto PR, Reineking B, Schröder B, Schurr FM, Wilson R (2010) Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. Ecography 30(5): 609–628. https://doi.org/10.1111/j.2007.0906-7590.05171.x

Duke NC, Meynecke JO, Dittmann S, Ellison AM, Anger K, Berger U, Cannicci S, Diele K, Ewel KC, Field CD, Koedam N, Lee SY, Marchand C, Nordhaus I, Dahdouh-Guebas F (2007) A world without mangroves? Science 317: 41–42. https://doi.org/10.1126/science.317.5834.41b

Enquist BJ, Norberg J, Bonser SP, Violle C, Savage VM (2015) Scaling from traits to ecosystems: Developing a general trait driver theory via integrating trait-based and metabolic scaling theories. Advances in Ecological Research 52: 249–318. https://doi.org/10.1016/bs.aecr.2015.02.001

Feller IC, Lovelock CE, McKee KL (2007) Nutrient addition differentially affects ecological processes of avicennia germinans in nitrogen versus phosphorus limited mangrove ecosystems. Ecosystems (New York, N.Y.) 10(3): 347–359. https://doi.org/10.1007/s10021-007-9025-z

Funk JL, Standish RJ, Stock WD, Valladares F (2016) Plant functional traits of dominant native and invasive species in mediterranean-climate ecosystems. Ecology 97(1): 75–83. https://doi.org/10.1890/15-0974.1

Gao D, Wang S, Wei F, Wu X, Zhou S, Wang L, Li Z, Chen P, Fu B (2022) The vulnerability of ecosystem structure in the semi-arid area revealed by the functional trait networks. Ecological Indicators 139: 108894. https://doi.org/10.1016/j.ecolind.2022.108894

Global Mangrove Alliance (2022) The State of the World's Mangroves 2022.

Guarino R, Chytrý M, Attorre F, Landucci F, Marcenò C (2021) Alien plant invasions in Mediterranean habitats: An assessment for Sicily. Biological Invasions 23: 3091–3107. https://doi.org/10.1007/s10530-021-02561-0

He N, Liu C, Piao S, Sack L, Xu L, Luo Y, He J, Han X, Zhou G, Zhou X, Lin Y, Yu Q, Liu S, Sun W, Niu S, Li S, Zhang J, Yu G (2019) Ecosystem traits linking functional traits to macroecology. Trends in Ecology & Evolution 34(3): 200–210. https://doi.org/10.1016/j.tree.2018.11.004

He N, Li Y, Liu C, Xu L, Li M, Zhang J, He J, Tang Z, Han X, Ye Q (2020) Plant trait networks: Improved resolution of the dimensionality of adaptation-science direct. Trends in Ecology & Evolution 35(10): 908–918. https://doi.org/10.1016/j.tree.2020.06.003

Holland OC, Stark JS, Wilson KA, Baker CM, Shaw JD, Helmstedt KJ (2025) Invasive species pose a threat to native species' abundances in an East Antarctic coastal marine ecosystems. Journal of Applied Ecology 62(8): 1993-2004. https://doi.org/10.1111/1365-2664.70062

Huang X, Yang Q, Feng J, Yang Z, Yu C, Zhang J, Ling J, Dong J (2022) Introduction of exotic species *Sonneratia apetala* alters diazotrophic community and stimulates nitrogen fixation in mangrove sediments. Ecological Indicators 142: 109179. https://doi.org/10.1016/j.ecolind.2022.109179

Li Y, Liu C, Xu L, Li M, Zhang J, He N (2021) Leaf trait networks based on global data: Representing variation and adaptation in plants. Frontiers in Plant Science 12: 710530. https://doi.org/10.3389/fpls.2021.710530

Li Y, He N, Liu C (2024) Plant functional trait networks: development of conceptual framework and advances in applications. Acta Ecologica Sinica 44: 7944-7961. [in Chinese with English abstract]

Li M, Ishfaq M, Quintero VAG, Peng D, Lang T, Gao C, Tam NF, Zhou H (2025) Impact of elevated environmental pollutants on carbon storage in mangrove wetlands: A comprehensive review. Ecological Indicators 178: 113830. https://doi.org/10.1016/j.ecolind.2025.113830

Michel P, Lee WG, During HJ, Cornelissen JHC (2012) Species traits and their non-additive interactions control the water economy of bryophyte cushions. Journal of Ecology 100(1): 222–231. https://doi.org/10.1111/j.1365-2745.2011.01898.x

Pan Y, Pan L, Qiu S, Qiu G, Su Z, Shi X, Fan H (2024) Variations in tree height among mangroves and their environmental adaptive mechanisms in China's coastal areas. Chinese Journal of Plant, Ecology 48: 483-495. [in Chinese with English abstract] https://doi.org/10.17521/cjpe.2023.0033

Parker JD, Burkepile DE, Hay ME (2006) Opposing effects of native and exotic herbivores on plant invasions. Science 311(5766): 1459–1461. https://doi.org/10.1126/science.1121407

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bretharte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas JG, De Vos AC, Buchmann N, Funes G, Quétier F, Hodgson JG, Thompson K, Morgan HD, Ter Steege H, Van Der Heijden MGA, Sack L, Blonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S, Cornelissen JHC (2013) New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany 61(3): 167–234. https://doi.org/10.1071/BT12225

Rao Q, Chen J, Chou W, Ren W, Cao D, Zhang M, Xiao H, Liu Z, Chen J, Su H, Xie P (2023) Linking trait network parameters with plant growth across light gradients and seasons. Functional Ecology 37(6): 1732–1743. https://doi.org/10.1111/1365-2435.14327

Reich PB, Cornelissen H (2014) The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. Journal of Ecology 102(2): 275–301. https://doi.org/10.1111/1365-2745.12211

Ren H, Lu H, Shen W, Huang C, Guo Q, Li Z, Jian S (2009) *Sonneratia apetala* Buch.Ham in the mangrove ecosystems of China: An invasive species or restoration species? Ecological Engineering 35(8): 1243–1248. https://doi.org/10.1016/j.ecoleng.2009.05.008

Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecology Letters 9(8): 981–993. https://doi.org/10.1111/j.1461-0248.2006.00950.x

Rosas-Guerrero J, Carmona R, Rosa JDL, Zanolla M, Altamirano M (2025) A population dynamics approach to understand the invasiveness of the seaweed *Rugulopteryx okamurae* (ochrophyta, dictyotales). NeoBiota 97: 1–17. https://doi.org/10.3897/neobiota.97.137873

Roscher C (2025) Competitive superiority of non-native invaders becomes weaker when plant diversity increases–a case study with *Solidago* species. NeoBiota 100: 239–256. https://doi.org/10.3897/neobiota.100.153209

Sobrado MA (2005) Leaf characteristics and gas exchange of the mangrove *Laguncularia racemosa* as affected by salinity. Photosynthetica 43(2): 217–221. https://doi.org/10.1007/s11099-005-0036-8

Solangi KA, Yang Z, Wei X, Solangi F, Zeng D, Liu L, Wang K, Zhang J, Song X (2025) Spatiotemporal assessment of mangrove cover, soil salinity, and nutrient patterns in Chengmai County using remote sensing (2018–2023). Ecological Indicators 178: 113877. https://doi.org/10.1016/j.ecolind.2025.113877

Verleye TJ, Kerkhove TRH, Hoey GV, Pirlet H, Kerckhof F, Lescrauwaet AK, Vandepitte L, Mees J (2025) National implementation of the European Union policy framework for monitoring introduced non-indigenous species in marine and brackish waters: A Belgian case study based on an updated species inventory. NeoBiota 103: 187–214. https://doi.org/10.3897/neobiota.103.159848

Walker B, Salt D, Reid W (2006) Resilience thinking: sustaining ecosystems and people in a changing world. Island Press, Washington, DC.

Wang YS, Gu JD (2021) Ecological responses, adaptation and mechanisms of mangrove wetland ecosystem to global climate change and anthropogenic activities. International Biodeterioration & Biodegradation 162: 105248. https://doi.org/10.1016/j.ibiod.2021.105248

Wang B, Yang S, Liu Q, Zhong C, Juma G, He F, Yang Y (2020) Artificial planting and natural spread of exotic mangrove species *Sonneratia apetala* and *Laguncularia racemosa* in Dongzhai Harbor, Hainan. Journal Article 39: 1778–1786. [in Chinese with English abstract]

Wang X, Ji M, Zhang Y, Zhang L, Akram MA, Dong L, Hu W, Xiong J, Sun Y, Li H, Degen AA, Ran J, Deng J (2023) Plant trait networks reveal adaptation strategies in the drylands of China. BMC Plant Biology 23(1): 266. https://doi.org/10.1186/s12870-023-04273-0

Wang X, Rahman MA, Cadotte MW, Mokroš M, Pauleit S, Rötzer T, Chen B, Liang X, Shen G, Wan Y, Dong X, Xu J, Da L, Song K (2025) Integrating forest inventory and LiDAR observations to uncover the role of plant traits on cooling and humidifying effects in urban area. Journal of Applied Ecology 62(8): 1953–1967. https://doi.org/10.1111/1365-2664.70102

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets Ü, Oleksyn J, Osada N, Villar R (2004) The worldwide leaf economics spectrum. Nature 428: 821–827. https://doi.org/10.1038/nature02403

Wright IJ, Dong N, Maire V, Prentice IC, Westoby M, Díaz S, Gallagher RV, Jacobs BF, Kooyman R, Law EA, Leishman MR, Niinemets Ü, Reich PB, Sack L, Villar R, Wang H, Wilf P (2017) Global climatic drivers of leaf size. Science 357(6354): 917–921. https://doi.org/10.1126/science.aal4760

Xun Y, Di X, Jin G (2020) Vertical variation and economic strategy of leaf trait of major tree species in a typical mixed broadleaved-Korean pine forest. Acta Phytoecologica Sinica 44(3): 730–741. https://doi.org/10.17521/cjpe.2019.0307

Yang J, Wu A, Li J, Wei H, Qin J, Tian H, Fan D, Wu W, Chen S, Tong X, Liu X (2024) Structured and unstructured intraspecific propagule trait variation across environmental gradients in a widespread mangrove. Ecology and Evolution 14(1): e10835. https://doi.org/10.1002/ece3.10835

Yang H, Zhang Z, Ding J, Li L, Tang Y, Feng J, Shi S (2025) Contrasting trait variations and trait correlation networks across heteromorphic leaves of *Populus euphratica.* Journal of Plant Ecology 18(2): rtaf025. https://doi.org/10.1093/jpe/rtaf025

Ye Z, Mu Y, Duzen SV, Ryser P (2024) Root and shoot phenology, architecture, and organ properties: An integrated trait network among 44 herbaceous wetland species. The New Phytologist 244: 337–340. https://doi.org/10.1111/nph.19747

Supplementary material 1

Basic information for each plot

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